# PHRYNIDAE (AMBLYPYGI) FROM ANDROS ISLAND, BAHAMAS, WITH NOTES ON DISTRIBUTION PATTERNS, RECENT ORIGIN AND ALLOMETRY

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**ABSTRACT:** Fieldwork on Andros Island produced two species of phrynid amblypygi, *Phrynus margine-maculatus* and *Paraphrynus viridiceps*. New localities and biological data are presented. The species were found to be completely sympatric in two of the three localities where they were collected. The presence of amblypygi in the Bahamas is attributed to Recent dispersal from Cuba via Paleoprovidence, a land mass which emerged during the lower sea-levels accompanying Pleistocene glacials. Dispersal from Florida and Hispaniola is rejected. Significant isometric or allometric relationships between median prosomal length and pedipalp tibia length were not detected. The work generally points to the lack of much basic information on amblypygid distribution and bionomics.

Two species of phrynid amblypygi are known from the Bahamas. *Phrynus marginemaculatus* C. L. Koch is widespread in the northern Bahama Islands (Quintero 1981) and *Paraphrynus viridiceps* (Pocock) is known from southern Andros and New Providence Islands (Banks 1906; Mullinex 1975). From published records, both appear to be uncommon to rare in the Bahamas. Furthermore, these species have never been recorded as being completely sympatric in the same habitat (see Quintero 1983).

The general lack of collecting of all arthropods in the Bahama Islands, and especially Andros Island, was noted by the author several years ago while undertaking literature searches. This was surprising because Andros Island is the largest island in the Bahamas (Fig. 1), and has the greatest diversity of vegetation types which would presumably harbor the greatest number of arthropod species in the Bahamas. As a result of a familiarity based on many trips to Andros Island the author decided to undertake an extensive survey of this island, employing modern mass collecting techniques not used by earlier workers. Recent collecting has revealed new localities and biological data for two Bahamian amblypygi species on Andros Island. This report is offered as a contribution to knowledge of the arthropods of the West Indies.

## METHODS

The project was intended as a general survey of the arthropods of Andros Island, thus a wide variety of collecting techniques were employed. Collecting efforts from May through August 1987 (110 days) used flight intercept traps, malaise traps, baited pitfall traps, shrub and tree beating, grass sweeping, blacklighting and hand collecting [the most successful in terms of obtaining amblypygi specimens]. The author was assisted by a technician throughout the collecting period. Intensive hand collecting included investigating all caves and "banana holes" found, which often required the use of rappelling equipment to gain entrance. In addition stones, rocks, leaf litter and logs were turned and the spaces beneath the bark of dead trees examined to a height of 2 m.

A large number of localities were sampled (>100) which included all the recognised vegetation zones many times over. Most recent plant ecology workers have characterized ten distinct Bahamian vegetation types; these are beach/ strand, coastal rock, coastal coppice, interior coppice, pineland, savanna, scrub, freshwater marsh, saltwater marsh, and mangrove (Nickrent et al. 1987).

All specimens recorded here were collected and identified by the author and vouchers were deposited by Dr. S. B. Peck (Department of Biology, Carleton University, Ottawa) in the arachnology collection of the American Museum of Natural History.

The significance of allometric changes in amblypygi has been previously studied and detailed by Quintero (1983) for seven Cuban species. The significance of allometric changes in Bahamian



Figure 1.—Map showing major islands of the Bahamas in relation to the Antilles and Florida. Line around islands represents probable extent of land area during Pleistocene glacial low sea levels. Paleoprovidence is the name proposed for the largest and most central of these Pleistocene glacial islands. Water barriers to dispersal were less significant during these times. Species may have been lost as sea levels rose, and the fauna was forced into today's more restricted island areas.

species has not been previously examined. Due to the small sample size, immatures, females and males were combined into a single data set (Table 1) as did Ouintero (1983). The relationship between median prosomal length (x) and pedipalp tibia length (y) was calculated using the Statgraphics simple regression package (Version 2.6). Both linear and multiplicative models were fit to the data. The best-fit model was chosen based on R-squared values with the final relationship between x and y expressed as a power curve  $[y = a x^{b}]$ . Comparison of actual and predicted slopes (Futuyma 1986), using the Student's t test, followed techniques suggested by Sokal & Rohlf (1981) and Hoel (1984). Interpretation of results adhered to methods proposed by Futuyma (1986) and Packard & Boardman (1987). Statistical data are presented in Tables 2 and 3.

## **RESULTS AND DISCUSSION**

Both *Phrynus marginemaculatus* and *Paraphrynus viridiceps* were found to be resident on Andros Island. Despite intensive and prolonged searching, populations were located in only three small (each roughly 0.5 km<sup>2</sup>) and isolated localities of high interior coppice. No specimens of either species were found in any of the other nine recognized vegetation zones. Only a few specimens of each species were collected so as not to disrupt what appeared to be uncommon and isolated populations. However, they were found to be very abundant throughout the period from May to August 1987. The two species bear the following information.

#### Phrynus marginemaculatus

Distribution.—This species has the most uppermost latitudinal distributional range of any amblypygid species in the eastern part of North America. It has been previously recorded from Bermuda, southern Florida, Cuba, Haiti, Dominican Republic, Puerto Rico, Jamaica, and Antigua (Quintero 1983) and is widespread in the northern Bahama Islands (Quintero 1981).

New Records.-BAHAMAS: Andros Island (random search of high interior coppices): CDC Farm, Cricket Coppice, 19 July 1987, 1 female; Shot-gun Coppice,

Table 1. – Measurements of Median Prosomal Length (x) and Pedipalp Tibia Length (y), in mm, from specimens collected from Andros Island during July 1987. A = Phrynus marginemaculatus, B = Paraphrynus viridiceps.

Specimen	A		В	
number	x	у	X	У
1	3.984	3.992	5.140	4.998
2	5.280	5.450	7.085	8.100
3	4.290	4.423	6.140	6.140
4	5.040	4.783	4.235	4.000
5	2.950	2.790	3.589	3.400
6	4.558	4.940	3.790	3.280
7	-	_	3.060	2.890
8	_	_	5.685	5.465

19 July 1987, 2 females (1 with 12 eggs), 4 males; London Ridge, 24 July 1987, 1 male.

**Variation.**—Body length 6.32–13.98 mm; median prosomal length 2.95–5.28 mm; left pedipalp tibia length 2.79–5.45 mm. Color varies from wheat yellow to black in both males and females.

#### Paraphrynus viridiceps

**Distribution.**—This species is limited to the Bahamas and Cuba (Quintero 1983). *Paraphrynus viridiceps* has been previously recorded from Cuba (Quintero 1983). The holotype male was collected in New Providence and described by Pocock (1893). Additional Bahamas records include Andros Island (South Bight) and New Providence (Mullinex 1975).

New Records.—BAHAMAS: Andros Island (random search of high interior coppices): CDC Farm, Cricket Coppice, 19 July 1987, 1 male; London Ridge, 24 July 1987, 4 females, 2 males, 1 immature.

**Variation.**—Body length 6.29–15.04 mm; median prosomal length 3.06–7.08 mm; left pedipalp tibia length 2.89–8.10 mm. Color varies from wheat yellow to black in both males and females.

Local Distribution and Habitat Preferences: High interior coppices occur on elevated parts of Andros Island. This community is the most diverse of the vegetation zones on the island. Dominant woody plant species in this vegetation zone include Bursera simaruba, Metopium toxiferum, Ficus aurea, Exothea paniculata, Calyptranthes pallens, Drypetes diversifolia, Clusea rosea, Psychotria angustifolia and Nectandra coriacea (Nickrent et al. 1987). The surface of the high coppice is very much eroded and slightly depressed which tends to accumulate moisture. They are protected from annual burning of the surrounding pine forests and savanna (the two most common vegetation zones). The canopy of a coppice is dense with a cool and wet, but sparse, understory layer. The vegetation grows on honey-combed limestone which affords the amblypygids many small holes in which to retreat. Amblypygi appear to favor cool, wet habitats (Quintero 1983) which explains their preference for the high interior coppice. The coppices are separated by wide stretches of arid savanna and pine forest. Two of the three coppices in which these species were found (London Ridge and Shotgun Coppice) lie approximately 60 km from each other. The third coppice (Cricket Coppice) is within four km of Shot-gun Coppice. Pocock (1893) recorded Paraphrynus viridiceps from southern Andros Island, which is over 100 km from the populations recorded here, and permanently separated by a wide salt-water gap from the central and northern sections of the island. Although amblypygids are known to run rapidly, their dispersal capabilities are unknown. No specimens were found in the dry savanna or pine forest. If non-habitable areas lie between coppices, then four km may be as much a barrier to gene flow as 60 km. At present it is not known if amblypygids disperse between coppices in the Bahamas, However, widespread habitat destruction has occurred several times on Andros Island as a result of logging; therefore, the present apparent isolation of these populations may be a recent condition.

Sympatry: Partial sympatry of species ranges between Phrynus and Paraphrynus has been reported previously (Quintero 1983). However, Quintero (1983) "doubts" that "species ranges will overlap to a major extent" due to "competitive exclusion". On Andros Island Paraphrynus viridiceps and Phrynus marginemaculatus were found to be completely sympatric in the same habitat. They were also observed to intermingle freely. However, these observations do not disprove the occurrence of competitive exclusion. The absence of specific information relating to specific niche requirements for either species makes it difficult to support or refute competitive exclusion.

Recent origin of Bahamian amblypygids: Three possible sources of Bahamian amblypygi must be considered. These are Florida, Cuba and Hispaniola. Dispersal of flora and fauna from Florida into the Caribbean is considered to be a very rare event. Many insect groups (Eick-

Sp.	Model	$a \pm SE$	$b \pm SE$	$R^2$	SE estimate
A A	L M	$-0.295 \pm 0.59 \\ -0.153 \pm 0.16$	$\begin{array}{c} 1.08 \pm 0.13 \\ 1.11 \pm 0.11 \end{array}$	94.18 95.92	0.250 0.053
B B	L M	$\begin{array}{c} -1.208 \pm 0.45 \\ -0.338 \pm 0.11 \end{array}$	$\begin{array}{c} 1.23  \pm  0.01 \\ 1.20  \pm  0.07 \end{array}$	96.89 97.81	0.335 0.057

Table 2. — Statistics for regressions of Median Prosomal Length (x) versus Pedipalp Tibia Length (y), comparing linear (L) and multiplicative (M) models. Data from specimens collected from Andros Island during July 1987. A = Phrynus marginemaculatus, B = Paraphrynus viridiceps, a = intercept, b = slope.

wort 1988—Halictidae; Liebherr 1988—*Platyn-us*; Nichols 1988—Scaratinae; Ramos 1988— Homoptera; Slater 1988—Lygaeidae; Wilson 1988—Formicidae; Peck 1989—south Florida insects) and trees (Tomlinson 1980) are believed to have dispersed from the Caribbean north, via Cuba or the Bahamas, to south Florida (Patterson & Stevenson 1977). The strong northern movement, from the southern Caribbean, of storms, prevailing winds and the Gulf Stream supports this argument. The author agrees with this assessment and with the implication that southern movement of flora and fauna from Florida to the Bahamas can be considered a very rare event.

Immigration and certain residency could have only been possible since the re-emergence of the Bahamas after Pliocene flooding. The northern Bahamas (including Andros Island) are part of the Bahama Bank, considered to be exposed continental shelf (Lee 1951; Burke et al. 1984; Donnelly 1988). During the lower (some 100 m) sealevels accompanying Pleistocene glacials and as recently as 18,000 years BP, the northern Bahamas were broadly and continuously adjacent to Cuba via a land mass known as Paleoprovidence, with the latter separated from the former by only a few kilometres of open water (Fig. 1). Immigration from Cuba during this time is the most likely route, rather than the "steppingstone" route from Hispaniola via the southern Bahamas. This hypothesis is reflected in the current distribution of Bahamian trees. Sixty-three species are common to the Bahamas and Cuba, while only twenty-nine are common to the Bahamas, Cuba, Hispaniola and the Lesser Antilles (Patterson & Stevenson 1977). Therefore the widespread presence of Phrynus marginemaculatus throughout the northern Bahama Islands and the more restricted distribution of Paraphrynus viridiceps to only a few of these islands is a reflection of a once widespread distribution of these species throughout Paleoprovidence. Rising sea-levels and inundation of most of Paleoprovidence have formed the present Bahama Islands in the last few thousand years. This reduction in area would also have reduced species numbers to present levels and restricted their movement between the newly isolated islands.

Allometry: Both the linear and multiplicative models had significant fits to the data for both species (Table 2). However, the R-squared values were higher for the multiplicative model, indicating that a power curve is the best-fit line.

Allometries between closely related species are not congruent; but significantly different interspecific differences between wild and laboratory reared specimens have been reported, although Quintero (1983) ascribes these differences to methodology. Quintero (1983) reported isometric growth for seven Cuban species of amblypygi. It is more probable that he proved allometric growth for reasons which are detailed below.

Demonstration of an allometric or an isometric relationship depends on the value of both the intercept and slope of the best-fit line. Packard & Boardman (1987), in their comprehensive review of allometric analysis, state: "When a plot of some variable of interest yields a straight line passing through the origin of a graph with linear co-ordinates, the variable varies isometrically with body size. When the line is curvilinear or when it does not pass through the origin, however, the variable varies allometrically with body size". Since neither line passes through the origin, the Bahamian amblypygi species in this study do not exhibit isometric growth (Table 2; Fig. 2). It is also evident that Quintero (1983) demonstrated allometric growth, rather than isometric growth, as none of the best-fit lines which he presented passed through the origin. This is not an unexpected finding since size-related variation in most physiological variables is allometric (Packard & Boardman 1987).



Figure 2.—Allometric growth curves with linear co-ordinates: Median Prosomal Length (abscissa) versus Pedipalp Tibia Length (ordinate), measurements in mm. Slopes of both graphs are not significantly different from one and therefore an allometric relationship is not demonstrated. A = Phrynus marginemaculatus, B = Paraphrynus viridiceps.

Species	t	N-2	Р
Phrynus marginemaculatus Paraphrynus viridiceps	0.246 0.529	4 6	$0.3 > P > 0.4 \\ 0.3 > P > 0.4$

Table 3.—Statistics for Student's t test to determine whether the slope of the multiplicative regression differs significantly from one for each of the Andros Island amblypygi species. If b = 1, then an allometric relationship is not demonstrated (Futuyma 1986). This is the case for both species.

While the data in this study did not exhibit an isometric relationship, it cannot be concluded that an allometric one is demonstrated by default. An allometric relationship also depends on the value of the slope (b) (Futuyma 1986). Allometry is demonstrated only if 1 < b > 1. If b =1, then v is a constant proportion of x and allometry is not demonstrated. This is the case with both species of Bahamian amblypygi from Andros Island (Table 3); therefore, allometry is not demonstrated. This is in contradiction to Quintero (1983) who reported an allometric relationship for the same variables in seven species of Cuban amblypygi. Quintero (1983) did not detail his methodology so no reason for this discrepancy can be determined at this time, save for disproportionate sample sizes.

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#### LITERATURE CITED

- Banks, N. 1906. Arachnida from the Bahamas. Bull. American Mus. Nat. Hist., 22:185–189.
- Burke, K., C. Cooper, J. F. Dewey, P. Mann, & J. L. Pindell. 1984. Caribbean tectonic and relative plate motions. Pp. 31-63. *In* The Caribbean-South American Plate Boundary and Regional Tectonics (W.E. Bonini, R. B. Hargraves, & R. Shagam, eds.). Geol. Soc. America Mem., 162.
- Donnelly, T. W. 1988. Geological constraints on Caribbean biogeography. Pp. 15–37. In Zoogeography of Caribbean Insects. (J. K. Liebheer, ed.). Cornell University Press, Ithaca, New York.
- Eickwort, G. C. 1988. Distribution patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae). Pp. 231–254. *In* Zoogeography of Caribbean Insects. (J. K. Liebheer, ed.). Cornell University Press, Ithaca, New York.
- Futuyma, D. J. 1986. Evolutionary Biology, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts. 600 pp.
- Hoel, P. G. 1984. Introduction to Mathematical Statistics. 5th ed. John Wiley and Sons, Toronto. 435 pp.
- Lee, C. S. 1951. Geophysical surveys on the Bahama Banks. J. Inst. Petrol., 37:633–657.
- Liebherr, J. K. 1988. Biogeographic patterns of West Indian *Platynus* carabid beetles (Coleoptera). Pp. 121–153. *In* Zoogeography of Caribbean Insects, (J. K. Liebherr, ed.). Cornell University Press, Ithaca, New York.
- Mullinex, C. L. 1975. Revision of *Paraphrynus* Moreno (Amblypygida: Phrynidae) for North America and the Antilles. Occ. Papers Calififornia Acad. Sci., 116:1–80.
- Nichols, S. W. 1988. Kaleidoscopic biogeography of West Indian Scaratinae (Coleoptera: Carabidae). Pp. 71–121. *In* Zoogeography of Caribbean Insects. (J. K. Liebherr, ed.). Cornell University Press, Ithaca, New York.

- Nickrent, D. L., W. H. Eshbaugh & T. K. Wilson. 1987. The vascular flora of Andros Island. University of Illinois, Urbana, Illinois. 182 pp.
- Packard, G. C. & T. J. Boardman. 1987. The misuse of ratios to scale physiological data allometrically with body size. Pp. 216–240. *In* New Directions in Ecological Physiology. (M. E. Feder, A. F. Bennett, W. W. Burggren & R. B. Huey, eds.). Cambridge University Press, Cambridge.
- Patterson, J. & G. Stevenson. 1977. Native trees of the Bahamas. Bahamas National Trust, Nassau. 128 pp.
- Peck, S. B. 1989. A survey of insects in the Florida Keys: Post-Pleistocene land-bridge islands: Introduction. Florida Ent., 72:603–612.
- Pocock, R. I. 1893. Contributions to our knowledge of the arthropod fauna of the West Indies. III. Diplopoda and Malacopoda, with a supplement on the Arachnida of the class Pedipalpi. J. Linn. Soc. Zool., 24:473–544.
- Quintero, D., Jr. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). J. Arachnol., 9:117–166.
- Quintero, D., Jr. 1983. Revision of the amblypygid spiders of Cuba and their relationships with the Ca-

ribbean and continental American amblypygid fauna. Studies on the Fauna of Curaçao and other Caribbean Islands, 196:1–54.

- Ramos, J. A. 1988. Zoogeography of the Auchenorrhynchous Homoptera of the Greater Antilles (Hemiptera). Pp. 61-71. *In* Zoogeography of Caribbean Insects. (J. K. Liebherr, ed.). Cornell University Press, Ithaca, New York.
- Slater, J. A. 1988. Zoogeography of West Indian Lygaeidae (Hemiptera). Pp. 38–61. *In* Zoogeography of Caribbean Insects. (J. K. Liebherr, ed.). Cornell University Press, Ithaca, New York.
- Sokal, R. R. & F. J. Rohlf. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. 2nd ed. W. H. Freeman and Co., San Francisco. 859 pp.
- Tomlinson, P. B. 1980. The Biology of Trees Native to Tropical Florida. Harvard University Printing Office, Allston, Massachusetts. 480 pp.
- Wilson, E. O. 1988. The biogeography of the West Indian ants (Hymenoptera: Formicidae). Pp. 214– 231. *In* Zoogeography of Caribbean Insects. Cornell University Press, Ithaca, New York.

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